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Zoological Research

ENERGY DENSITY, WATER CONTENT AND THEIR VARIATIONS IN CARNIVOROUS AND HERBIVOROUS BEETLES

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Abstract. The energy density, water content and their variations of adult coleopteran insects were studied by determining carnivorous Carabidae and herbivorous Tenebrionidae in arid environment. The energy density of carnivorous Carabidae (22.64 J/mg AFDW) was significantly higher than herbivorous Tenebrionidae (20.55 J/mg AFDW), but their difference in water content (54.96% and 63.28% respectively) was converse ($P<0.05$). The energy density in these two families of beetles correlated negatively to their water content ($r=-0.5962$, $P<0.05$). Both the energy density and water content of these coleopteran insects exhibited significantly seasonal variations, in which the energy density was found maximum in autumn (22.80 J/mg AFDW) and minimum in spring (20.42 J/mg AFDW), conversely, the water content was lowest in autumn (54.93%) and highest in spring (61.88%) ($P<0.05$). The energy density of different parts of body in these beetles also showed significant variations in which the energy density was highest in abdomen (22.65 J/mg AFDW) and then decreased in thorax (21.33 J/mg AFDW), head (20.89 J/mg AFDW) and legs (20.60 J/mg AFDW), and similarly, found maximum in autumn (22.30 J/mg AFDW) and minimum in spring (19.46 J/mg AFDW). The energy density of Carabidae and Tenebrionidae insects correlated positively to the energy density in their abdomen, thorax, head and legs (r values were 0.897, 0.846, 0.718 and 0.604 respectively, $P<0.05$) in which the correlation coefficients of abdomen and thorax were significant higher than head and legs ($P<0.05$). This results implied that main reason for the high energy density in beetles was the accumulated lipid in abdomen and thorax. In addition, the factors that affect the variations of energy density and water content, and the effects of these variations in these prey beetles on the food selection of insectivorous predators were also discussed.

Key words. Energy density, Water content, Food habit, Beetle

Insects of the families Carabidae (Coleoptera: Adephaga) and Tenebrionidae (Coleoptera: Polyphaga) occur widely throughout the world and occupy most terrestrial environments. Carnivorous Carabidae and most of herbivorous Tenebrionidae beetles are usually ground-dwelling, with relatively low flight ability in comparison with other insects, and thus are accessible and become the major prey for insectivorous predators, especially for the insectivorous mammals (Fisher *et al.*, 1993; Chen *et al.*, 1998).

Current concepts of optimal foraging theory frequently suggest and assume that prey selection are primarily based on the maximization of energy intake in relation to the cost of searching, capturing, handling and consuming the prey (Stephens *et al.*, 1986). The essential in studies of optimal foraging is to determine the specific amount of energy that a prey will return to a predator and the energetic costs of foraging. Moreover, energy is the most popular currency for studying the energy flow and for quantitatively evaluating the relationships between various living components in ecosystem. Therefore, the energy density measurements of insects and other biological materials become a fundamental and necessary work for the studies of not only prey selection but also energy flow. Golley (1961) and Cummins *et al.* (1971) ever cautioned that energy density of biological materials were influenced by many factors and must be determined under the specific conditions for one's particular study. However, far fewer researchers have

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studied the variation of insect energy density (Brooks *et al*., 1996; Kumar, 1996).

In arid environment, drought is the most obvious characteristic, and deficiency of water is also the primary challenge to survival by mammals even if the mammal solves the problem of obtaining adequate nutrients (Nagy, 1994). In order to make the following questions clear, we provide a detailed analysis of the variations in energy density and water content of Carabidae and Tenebrionidae insects collected over a four-season period between 1996 and 1997 in arid environment. (1) Does the energy density or water content vary significantly in these two taxonomic groups which have the different food habits? (2) Does the energy density or water content change seasonally? (3) Is there any difference between the energy density of different body parts of Coleoptera? (4) Is there any correlation with these variations in energy density and water content? These results will provide valuable references for the future studies on prey selection of insectivores or energy flow in arid environments, also.

1　Study Area and Methods

1.1　Study area

This study was conducted in Ethabuka Station in the eastern Simpson Desert, Queensland (23°46′N, 138°25′E), where leached, sand soils with parallel sandy ridges are characterised. *Triodia basedowii* and *Acacia cambagei* are dominant vegetation (Dickman *et al*., 1993).

1.2　Insect collection

Adult beetles were collected during four periods, the middle of September, 1996 (spring, raining and cold), the middle of November, 1996 (early summer, dry and hot), the end of April, 1997 (autumn, after rainfall, warm) and the middle of June, 1997 (winter, dry and cold), from the same site. The beetles were captured in pitfall traps or by hand in the same site primarily at night, and then taken back to the laboratory alive by methods described by Zborowski *et al*. (1995).

1.3　Measurement of energy density

Individual adult insects were placed into tared jars, weighed and killed by freezing within two collection days from the field, and then dried to constant mass at 60℃ (Norberg, 1978; Kumar, 1996), water content was calculated. The animals were identified to the species in family (Hawkeswood, 1987; CSIRO, 1991). Major body parts of the insects were separated under an Olympus CH—2 stereo microscope, and each body part of each insect was weighed. Each sample of body part was ground in a mortar pestle and the powder pressed into a pellet of approximately 10 mg with distilled water. For small insects, it was necessary to pool the same body parts from different individuals of same species to make a pellet of at least 5 mg (Cummins *et al*., 1971).

The pellets were dried again at 60℃ in the oven for at least 12 hours and then cooled and reweighed. Determination of energy density was carried out by a Phillipson Oxygen Microbomb Calorimeter (Gentry Instrument, Inc.), coupled to a SP—G3C Speedex chart recorder (John Morris Scientific Pty Limited). The calorimeter was recalibrated after every 30 analyses by burning pellets of benzoic acid. The ash content in each sample was determined by weighing after each test.

1.4　Data analyses

Energy values were expressed as J/mg of ash-free dry mass (J/mg AFDW).

For relevant comparisons, one-way analyses of variance (ANOVA) and the Student-Newman-Keuls' multiple range test (SIGMASTAT of Jandel Scientific for Windows, version 1.0) were used. The t-test was performed to determine whether the significance of the correlation was significant, the significant level is 0.05.

2　Results

2.1　Energy density in different families

The energy density of Carabidae and its dry body mass was significantly higher than Tenebrionidae respectively ($P < 0.05$). The mean water content in Carabidae was significantly lower than Tenebrionidae ($P < 0.05$). No significant difference was found between the ash contents in different families (Table

1).

Table 1 Energy density and water content in Carabidae and Tenebrionidae

Family	Energy density/ $J \cdot mg^{-1}$ AFDW ($n=71$)	Water content/ % ($n=82$)	Ash content/ % ($n=84$)	Body mass/mg ($n=85$)
Carabidae	22.64^{a}±1.63	54.96^{a}±5.74	0.184±0.58	282.85^{a}±330
Tenebrionidae	20.55^{b}±1.56	63.28^{b}±6.58	0.947±3.05	144.19^{b}±132
Mean	21.91 ±1.89	57.90 ±7.22	0.452 ±1.88	233.91 ±282

Values (mean± *SD*) with different small letter (a, b) are significantly different between families ($P<0.05$).

2.2 Seasonal variations of energy density in families

The energy density in coleopteran insects showed significantly seasonal variations and their variation tendency was similar in both families (Fig. 1). The mean energy density was highest in autumn (22.80 J/mg AFDW), and lowest in spring (20.42 J/mg AFDW). Mean energy density in autumn and summer were all significantly higher than that in spring ($P<0.05$).

2.3 Energy density of different parts of the body in coleopteran insects

Energy densities of different parts of the body were significantly different (Table 2). The energy density of abdomen was significantly higher than others ($P<0.05$).

Table 2 Energy density of different parts of body in Carabidae and Tenebrionidae

Family	Energy density/ $J \cdot mg^{-1}$ AFDW			
	Abdomen ($n=51$)	Thorax ($n=51$)	Head ($n=41$)	Legs ($n=41$)
Carabidae	23.32^{a}±2.01	21.94^{b}±2.26	21.60^{b}±1.56	21.01^{b}±2.11
Tenebrionidae	21.25^{a}±1.56	20.13^{b}±1.46	19.40^{b}±2.78	19.75^{b}±1.31
Mean	22.65^{a}±2.10	21.33^{b}±2.19	20.89^{b}±2.27	20.60^{b}±1.96

Values (mean± *SD*) with different small letter (a, b) are significantly different between different parts of the body ($P<0.05$).

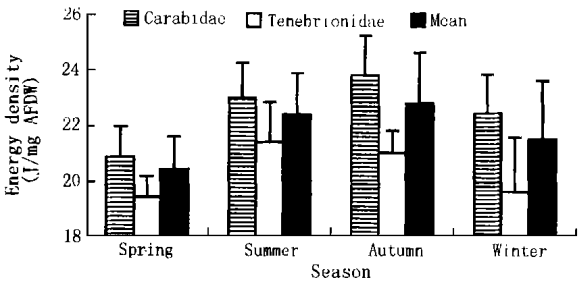

Fig. 1 Seasonal variations of energy density (mean± *SD*, $n=71$) in beetles

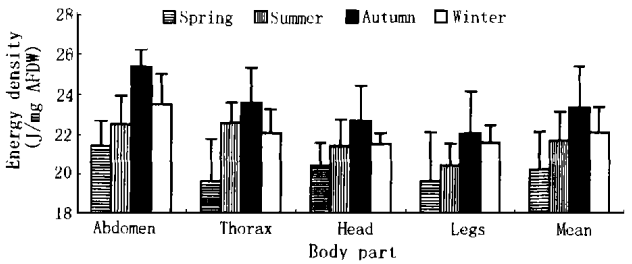

Fig. 2 Seasonal variations of energy density (mean± *SD*, $n=184$) in different parts of body

2.4 Seasonal variations of energy density in different parts of body

The energy density in different parts of body varied seasonally and their variation tendency was similar in abdomen, thorax, head and legs (Fig. 2). The mean energy density of different parts of body was highest in autumn (22.30 J/mg AFDW), middle in summer (20.93 J/mg AFDW) and winter (20.76 J/mg AFDW), and lowest in spring (19.46 J/mg AFDW). Mean energy densities of different parts of body in autumn, summer and winter were all significantly higher than spring, and mean energy density of different parts of body in autumn was significantly higher than both summer and winter ($P<0.05$).

2.5 Relationship of energy density and water content

The energy density in Carabidae and Tenebrionidae was negatively correlated with their water content (correlation coefficient, $r=-0.5962$, $P<0.05$). The water content showed significantly seasonal variations (Fig. 3), in which those in autumn (54.93%) and summer (57.09%) were significantly lower than spring (61.88%) ($P<0.05$).

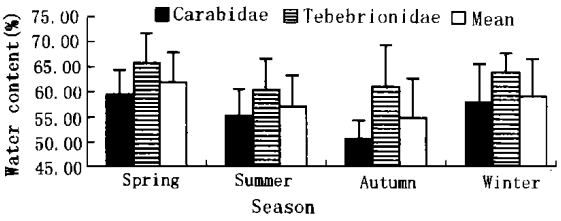

Fig. 3　Seasonal variations of water content (mean±*SD*, $n=91$) in Carabidae and Tenebrionidae

2.6　Energy density relationship between individual insects and different parts of body

The energy density of whole individual was significantly correlated with those of different parts of body ($P<0.05$). There is no correlation between energy density and body weight of the two families ($P>0.05$).

3　Discussion

Carabidae and Tenebrionidae beetles are mainly carnivorous and herbivorous respectively. Our data on the energy density of Carabidae and Tenebrionidae beetles showed that carnivorous beetles had higher energy density and lower water content than herbivorous beetles ($P<0.05$). The potential reason to explain these results was that these differences of energy density arose from differences in food availability of the carnivorous beetles to herbivorous beetles. Some previous studies investigated energy density variation in animals showed that the differences of energy density between the herbivores and carnivores can be found in the molluscs, insects and crustaceans and they have found high energy density of the species being an adaptation to an unpredictable food supply (Slobodkin *et al.*, 1961; Griffiths, 1977). Seasonal variations in the availability of food resources are much less for the herbivores than they are for the carnivores, and thus the carnivores should store more energy than the herbivores to meet future nutritional stresses (Griffiths, 1977). Energy is usually stored as lipid which, because of its much higher energy density than protein or carbohydrate, results in higher energy density of the carnivores. As Slobodkin *et al.* (1961) suggested, natural selection favoured the species with high energy density having accumulated energy (as lipid) for some unfavourable period in the life cycle.

The energy density of both carnivorous Carabidae and herbivorous Tenebrionidae beetles varied seasonally and was maximum in warm, rainy autumn. These results conformed that energy density of coleopteran insects varied seasonally (Cummins *et al.*, 1971; Kumar, 1996), but further suggested that in arid environment, not only seasonal temperature, but also the availability of abundant food after raining, be related to changes of physiological conditions and energy storage of insects. Species living in unpredictable environments where the food supply and other conditions varies greatly should store energy in favorable circumstances for meeting future stress and this results in their energy density should be more variable (Slobodkin *et al.*, 1961; Griffiths, 1977).

Energy density variations are also related to the developmental and reproductive stage of the animal. The life stage can make changes in lipid, protein and carbohydrate content and cause great seasonal variation in energy density. The energy density within the life cycle of an invertebrate species is high at the egg stage and prior to breed. These higher values can be principally attributed to the increase of lipid reserves (Cummins *et al.*, 1971). This study found that the energy density of both carnivorous Carabidae and herbivorous Tenebrionidae beetles had the same seasonal variation tendency as their different parts of body, and was correlated positively to the energy density of abdomen, thorax, head and legs ($P<0.05$) but negatively to their water content ($P<0.05$).

Carabidae and Tenebrionidae beetles are mostly ground-dwelling and easily accessible to mammalian insectivores. According to the optimal foraging theory, predators should maximize the net rate of energy intake during their foraging (Stephens *et al.*, 1986). Mammalian insectivores selecting Carabidae and Tenebrionidae beetles as their preys may decrease their energetic cost in foraging. This study found that the high energy density of Carabidae beetles and high water content of Tenebrionidae beetles further suggested that Carabidae and Tenebrionidae prey might return the large amount of energy and water to their

predators, respectively. Moreover, the result of present study showed that energy density of coleopteran insect varied due to season, and different parts of body also suggested that insectivores may shift their prey seasonally and select different body parts for maximizing the net rate of energy intake. Further relative feeding experiments should be conducted for the testing.

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不同食性甲虫的含能值、含水量及其变动规律研究

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摘要：以干旱地区的肉食性步甲科（Carabidae）和植食性拟步甲科（Tenebrionidae）昆虫成体为材料，测定鞘翅目甲虫的含能值和含水量，分析其含能值和含水量的相互关系及其变动规律。结果表明，肉食性步甲科昆虫的含能值（22.64 J/mg 无灰干重）显著高于植食性拟步甲科昆虫（20.55 J/mg 无灰干重）（$P<0.05$），相反，前者的含水量（54.96%）却显著地低于后者（63.28%）（$P<0.05$）。步甲科和拟步甲科昆虫的含能值都与其含水量成显著负相关（$r=-0.5962$，$P<0.05$）。步甲科和拟步甲科昆虫的含能值或含水量具有明显的季节变动规律，两科的变动规律基本相同，其中，含能值在秋季最高（22.80 J/mg 无灰干重），春季最低（20.42 J/mg 无灰干重），含水量则相反，秋季最低（54.93%），春季最高（61.88%）（$P<0.05$）。步甲科和拟步甲科昆虫的头、胸、腹和附肢不同体区的含能值具有显著差异（$P<0.05$），其中，腹部的含能值最高（22.65 J/mg 无灰干重），其次为胸部（21.33 J/mg 无灰干重），头部和附肢的含能值最低（20.89 J/mg 无灰干重和 20.60 J/mg 无灰干重）。不同体区的含能值也具有同样的季节变动，即含能值在秋季最高（22.30 J/mg 无灰干重），春季最低（19.46 J/mg 无灰干重）（$P<0.05$）。步甲科和拟步甲科昆虫的个体含能值与其头、胸、腹和附肢各体区的含能值成正相关，相关系

数分别为 0. 718、0. 846、0. 897 和 0. 604（$P<0.05$）；其中个体含能值与腹部或胸部体区含能值的相关系数显著地高于它们与头部和附肢含能值的相关系数（$P<0.05$）；这些结果说明，脂质在甲虫腹部和胸部的积聚是引起甲虫个体含能值提高的主要原因。本文对不同食性甲虫含能值产生差异的原因，甲虫含能值和含水量变动的影响因素也进行了分析；并结合最佳摄食理论，就甲虫作为猎物，其含能值和含水量的这些变动规律对食虫动物食物选择所可能产生的影响也进行了探讨，就今后进一步检验食虫动物摄食对策所应开展的猎物喂养食虫动物的实验提出建议。

关键词：含能值，含水量，食性，甲虫
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简　讯

胡列也吐的鹤类

胡列也吐位于内蒙古自治区呼伦贝尔盟陈巴尔虎旗境内，海拉尔市西北部 120 km。地理位置在东经 49°48′，北纬 118°27′，中俄边境地区。总面积 40 km^2。该区地势平坦，既有广阔的草原又有大面积的浅水湖泡和芦苇沼泽。在胡列也吐共有 5 个面积较大的泡子由西向东一字排列。本地区因地处中俄边境，人为干扰很小，区内仅有十几户牧民，无任何污染。此区水丰草肥，食物丰富，还有大片的苇塘，为水禽提供了良好的觅食地和隐蔽场所。每年均有数十万只水鸟来此栖息繁衍。亦是鹤类的最佳栖息地。1998 年 1 月～9 月笔者对该地进行了为期 4 个月的考察。考察中共统计到鹤类 4 种计 78 只。

白头鹤（*Grus monacha*）在胡列也吐为夏候鸟。6 月 23 日下午 16：00 在距胡列也吐东北 7 km 处的草原上发现了 47 只白头鹤，分成 3 群悠然自得地在草原上觅食，游荡。这 3 群分别为 4、19 和 24 只。每群之间的距离均为 2 km 以上。每个大群又由数个小群组成，19 只的白头鹤群是由 4 个小群构成的。个体数量分别为 3、8、7 和 1 只。每个小群之间的距离为 200～1 000 m。个体之间的距离为 5～100 m。每个大群最外端两只鹤之间的距离达 3 km。当笔者乘吉普车向鹤群靠近时，吉普车最近可靠近鹤群 50 m 左右。由于吉普车的冲击，鹤群向北移动了约 2 km，3 群鹤合成 1 群。群体内个体间的距离缩小。当吉普车再向鹤群靠近时，鹤群在吉普车距其 1 km 时，纷纷向北飞离。在回来的路上，在湖泡中 1 群 5 只白头鹤又飞起也向北飞去。6 月 25～30 日笔者又分别见到了 24、22 和 11 只的白头鹤集群。通过观察未发现该群内有雏鸟，只有 5～8 只为亚成体。

丹顶鹤（*Grus japonensis*）在胡列也吐为夏候鸟。每年均有繁殖个体。4 月 21 日在胡列也吐三泡子北岸发现 4 只迁徒群，4 只均为成体，在泡子的浅水处觅食。6 月 24 日在三泡子北岸发现 2 只丹顶鹤（1 成 1 幼），每日到北岸长有稀疏水草、水深在 5～20 cm 的泥滩中觅食。直到 7 月份因阴雨连绵，它们才迁往他处。9 月份迁徙期见丹顶鹤 2 群 5 只，分别为 1 成，2 成 2 幼。

白枕鹤（*Grus vipio*）本区未见有白枕鹤繁殖。只是在秋季迁徙季节见一群 4 只白枕鹤在四泡子东岸浅水草甸觅食，4 只鹤均为成体。当笔者乘吉普车向它们靠近约 1 km 时，它们由东岸飞到西岸，这群鹤在本区停留 3 d 后飞离。

灰鹤（*Grus grus*）在本区有分布，但数量极少。据当地牧民讲每年春季迁徙季节可见 5～10 只，但近 1～2 年未见。笔者在考察中亦未见到灰鹤。

蓑羽鹤（*Anthropioides virgo*）在鹤类中是体型最小的种类，在呼伦贝尔亦属最常见的鹤类。笔者曾于 1987 年 8 月在新巴尔虎左旗新宝力格东苏木见到 1 100～1 150 只的集群。但在胡列也吐数量则很少，仅在春天迁徙季节见到 2 群 11 只（4 只和 7 只）。

关键词：胡列也吐，鹤类
中图分类号：Q959. 726

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